THE PANORPOID COMPLEX.

A Study of the Phylogeny of the Holometabolous Insects, with Special Reference to the Subclasses Panorpoidea and Neuropteroidea. [Introduction].

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Introduction.

Section i.—Definition of the Complex.

In his great work upon the Phylogeny of the Orders of Insects. Handlirsch (2) divides the whole of the Holometabola into four Sub-classes, as follows:—

Sub-class.	Orders.
Hymenopteroidea	Hymenoptera.
Coleopteroidea	Coleoptera.
Neuropteroidea	Megaloptera, Raphidioidea, Neuroptera.
Panorpoidea	Panorpatæ, Phryganoidea, Lepidoptera, Diptera, Aphaniptera.

In making this division, Handlirsch widely separates the first two of these Sub-classes from the last two, placing between them not only what we may, for convenience, term the three Amphibiotic Orders (Odonata, Plectoptera, and Perlaria), each of which he elevates to the rank of a Sub-class, but also the Embidaria, which he also considers to be a Sub-class. For the Hymenopteroidea and Coleopteroidea, Handlirsch indicates a descent from a Blattoid type of ancestor. For the Neuropteroidea and Panorpoidea, he is more inclined to a Palæodictyopterous type of ancestor; indeed, he definitely states his belief that the Neuropteroidea are descended directly from the Palæodictyoptera, while he considers the Panorpatæ, and hence the Panorpoidea also, to have been derived from the obscure Megasecoptera of the Upper Carboniferous – an Order which, at the best, can be regarded only as a specialised side-branch of the Palæodictyoptera.

We are thus faced with the fact that, in Handlirsch's opinion, the Holometabola are a composite group of polyphyletic origin. Such a view is, indeed, fairly generally held amongst entomologists; for no satisfactory reason seems to have been brought forward why the evolution of the resting-pupa should not have been accomplished more than once, along several quite distinct lines of ascent.

Having for a very long time carefully read and studied Handlirsch's views, I have to confess that, in spite of many excellent arguments brought forward, there seems to me to be much that is unsatisfactory in them. As examples, I might refer to his discussion of the origin of the Hymenoptera, which fails to convince me in a single point. The same may be said of the suggestion that the Panorpatæ are derived from the Megasecoptera. It seems to me that any unbiassed student of the Phylogeny of the Holometabola must come to the following conclusions :—

(1) That the origin of the Hymenoptera is still about as great a mystery as it well can be; and that Handlirsch's solution of this problem has many inherent defects that make it unacceptable.

(2) That the origin of the Coleoptera from a Blattoid type of ancestor is a fair probability; but that much more research of an intensive character must be carried out before this theory can be either proved or disproved.

(3) That the origin of the Neuropteroidea from Palæodictyopterous ancestors is extremely probable; nevertheless here also any researches that tend to strengthen the argument would be very welcome.

(4) That the origin of the Panorpoidea from the Megasecoptera is not supported by a single piece of evidence worth considering; but that the possibility of the relationship between Neuropteroidea and Panorpoidea being exceedingly close requires reconsideration, and the coincident possibility of the Panorpoidea

having had Palæodictyopterous ancestors also requires careful investigation.

My own researches upon the Neuropteroidea and Panorpoidea, as far as they have gone, have convinced me that these two Sub-classes have a great deal in common. They have also revealed the possibility of the Hymenoptera, and even the Coleoptera, having a closer relationship with the Panorpoidea than is generally suspected. Not only do many signs point to the Mecoptera (Panorpatæ) as being a central Order round which all the rest of the Holometabola may be more or less closely grouped, but the Palæontological evidence also points unmistakably in the same direction. For fossil Mecoptera of the genus *Permochorista*, closely allied to the existing Australian genus *Tæniochorista*, have now been proved to exist in the Permian of Newcastle, New South Wales(**6**); whereas no other Holometabolous insects are known from Palæozoic strata at all. Even admitting the incompleteness of the fossil record, we must be immediately struck with the fact that the Mecoptera existed in Permian times in Australia, in a form very similar to that of to-day. This points to the Order having arisen well before Permian times. The earliest known Neuropteroidea are Upper Triassic, the earliest Coleoptera also Upper Triassic, the earliest Trichoptera the same, and the earliest Hymenoptera Upper Jurassic. Even if we grant that it is a reasonable expectation that all these Orders will one day be found to have had representatives in earlier strata, yet the same probability holds for the Mecoptera.

Reviewing the whole case, it seems to me that the time is ripe for a careful study of the whole problem, as far as the evidence will admit, from the point of view of the Mecoptera as the central Order; that is to say, the Order which has preserved, both in its larval, pupal, and imaginal structures, the largest number of archaic characters derived from the original ancestor or ancestors of the Holometabola, whatever they may have been.

It is to suggest this point of view that I have selected as title the somewhat elastic term "The Panorpoid Complex." By this title, I intend to convey that the research entered upon in this paper has, for its main object, the complete working out of the relationships of the Order Mecoptera to those other Orders which stand in closest relationship to it. In accepting Handlirsch's division of the Holometabola into four Sub-classes, it is to be understood that I do so only provisionally, for the convenience of sifting and allocating the evidence that this arrangement naturally offers. And, as it is obvious that the main weight of the argument must centre around those Orders which are clearly most closely associated with the Mecoptera, so it will be clear that the Orders comprising the Panorpoidea must be most fully reviewed. There is, however, a great deal of evidence to be obtained from a study of the Neuropteroidea; and this Sub-class can by no means be denied full consideration in the argument. With respect to the Coleoptera and the Hymenoptera, the evidence to be obtained from them at the present time is comparatively scanty, and has little weight compared with that derived from the other Orders, though it may help to throw some light upon the larger problem of the origin of the Holometabola as a whole. These ideas I have tried to convey in the sub-title selected for this paper.

If, then, we accept provisionally, for clarity of argument, the two Sub-classes Neuropteroidea and Panorpoidea, in the sense that Handlirsch defined them (but with some modifications in the nomenclature of the Orders composing them), we may then proceed to define the "Panorpoid Complex" as *that assemblage of Orders whose ancestral characters can be shown to possess close affinity with the characters preserved to a great measure in the Order Mecoptera*, without in any way binding ourselves to the inclusion of any particular Order in the Complex. The Complex itself is an elastic assemblage of Orders; and any particular Order may be included in it, or removed from it, according as the weight of evidence may determine.

Throughout this paper, I shall use the name Mecoptera for the Panorpatæ of Handlirsch, and Trichoptera for his Phryganoidea. The Raphidioidea I hold to be not sufficiently distinct from the Megaloptera to deserve ordinal rank, since van der Weele's work (**7**) indicates the strong probability of their origin from the more ancient Sialoid stem. Hence I shall merge them into the Order Megaloptera, which will then consist of two Sub-orders, viz , the Sialoidea (aquatic) and the Raphidioidea (terrestrial). The term Neuroptera is now so ambiguous, being still used in present-day writings to indicate so many different and heterogeneous groups of Orders, that I have no hesitation, for the sake of clearness of argument, in substituting the name Planipennia for it, although I do definitely subscribe to the opinion that the name Neuroptera ought by now to be strictly confined to this Order only.

For the purposes of this paper, I shall definitely include my new fossil Order, Protomecoptera, within the Sub-class Panorpoidea, to which it clearly belongs. The type (and so far the only representative) of this Order is *Archipanorpa magnifica* Tillyard, from the Upper Trias of Ipswich, Queensland. Whether this type should constitute a new Order, or only a Sub-order within the Order Mecoptera, it will undoubtedly conduce to clarity of argument if we employ the term Protomecoptera in the sense in which I originally defined it(**5**).

The scheme adopted in this paper may now be exhibited as follows :—

Sub-class PANORPOIDEA :

Orders Protomecoptera (fossil only), Mecoptera, Trichoptera, Lepidoptera, Diptera, and Aphaniptera.

Sub-class NEUROPTEROIDEA :

Orders Megaloptera (including the aquatic Sub-order Sialoidea, and the terrestrial Sub-order Raphidioidea) and Planipennia (= Neuroptera, *s.str.*).

Section ii.—GENERAL PRINCIPLES.

Most of the work that has been done in Entomology upon the Phylogeny of any given Order has naturally been carried out by experts upon the Order in question, with little reference to outside Orders. As an example of this, we may cite Meyrick's numerous works on the Lepidoptera, which, apart from their systematic aims, have also attempted to show the origin of the Order, as a whole, from the Trichoptera. In the whole of this work, Meyrick makes allusion to only one genus (*Rhyacophila*) of the supposedly ancestral Order, and, indeed, suggests, in more than one place, that the whole of the Lepidoptera are descended from this still existing and abundant genus of Caddis-flies. Throughout the work, the characters of the Lepidoptera are subjected to a searching scrutiny and criticism, but the same tests are not applied to the Trichoptera, which are, nevertheless, an equally important factor in the problem [**3**, **4**].

It has, for long, seemed to me that a problem of this kind, attacked in this manner, *i.e.*, by intensive study of the internal differences within the Order in question, without an equally intensive study of the differences existing within the Orders supposedly ancestral to it, could not possibly yield a complete and accurate solution. The alternative, chosen by some few authors in recent years, has been to pass in review the supposedly archaic characters of related Orders, and to attempt to derive from this evidence some idea as to the standing of one Order to another. As an example of this, I need only mention again Handlirsch's famous attempt to give us a complete Phylogeny of the whole of the Orders of Insects, as well as a Phylogeny of the Class Insecta itself (**2**).

It will be at once admitted that this second method is the right one. It has, however, one obvious disadvantage. In order to carry it out successfully, the author should be equally expert upon all the Orders that he reviews. But no man could hope to attain the knowledge in half-a-dozen or more Orders that can be attained in one by a life-study of it. Hence we see that, while the outlook of such an author will be a broader one than that of the expert in one Order only, yet the evidence brought forward cannot all be accepted at the same face-value; and the chances of misinterpretations at vital points is evidently very much greater.

As an example of this, we might contrast the treatment of the Phylogeny of the Lepidoptera by Meyrick on the one hand, and by Handlirsch, on the other. First of all, Meyrick confines himself almost entirely to wing-venation. By an exceedingly full analysis of the different types within the Order, he arrives at the conclusion that the homonomously-winged Jugatæ represent the oldest type, within the Order. Having then discovered, in the living genus *Rhyacophila* of the Order Trichoptera, a venation with apparently all the essential characters of the Jugatæ, he claims that the Jugatæ, and therefore all the Lepidoptera, are to be regarded as having had a Rhyacophilous ancestor.

If the characters considered by Meyrick were the only ones that concerned the question, and if the Orders Trichoptera and Lepidoptera were so isolated from all the other Orders of Insects that there could be no question of affinities in any other direction, Meyrick's solution might be accepted as correct, in spite of its having been based mainly upon the wing-venation only. But this is not the case. As we shall see, the Order Mecoptera has quite equal, if not superior, claims to be regarded as the ancestral type from which the Lepidoptera sprang, while the claims of the Planipennia, in certain directions, may by no means be overlooked. Moreover, no attempt was made to test the claim, which surely can legitimately be made, that the Trichoptera themselves are a by no means unspecialised Order, with almost as much right to being considered an end-term in a Phylogenetic Series as the Lepidoptera themselves.

Many of these objections to the method of procedure adopted by Meyrick are overcome by the method which Handlirsch followed. This author, first of all, considers the relationships of the Trichoptera with the Mecoptera, and concludes that the former are an offshoot of the latter. He then propounds the question as to whether the Lepidoptera are to be legitimately regarded as the derivatives of the Trichoptera themselves, or whether we are compelled to go further back, to the older Mecoptera, in order to indicate their ancestors. His review of this question is, in its way, a masterly exposition of the facts, as far as he knew them; and his conclusion, that the Lepidoptera are not descended from the Trichoptera, but directly from the older Mecoptera, cannot fail to commend itself to all biologists, if the facts that he quotes are really correct.

Here, then, comes in the question which I have already mentioned, viz., the amount of equipment of specialised knowledge of all the Orders taken into consideration, necessary for an author who would decide this problem. Having carefully read through the whole of Handlirsch's work, I was at once struck with his evident lack of specialised knowledge of the two Orders most fundamental to the whole question, viz., the Trichoptera and the Mecoptera. The characters of these two Orders are reviewed very superficially in comparison with those of the Lepidoptera and Diptera; in fact, the whole of their phylogeny is decided within the limits of a single page of print. And, on that one page, I find statements made which, as far as my knowledge of these Orders goes, are incorrect. Such, for example, is the statement on p 1254, that the jugum appears in the Mecoptera as well as in the Lepidoptera, and that on p.1253, that the Mecoptera retain the archaic homonomous wings and archaic mouth-parts. In my studies of the Mecoptera, I have found that none of these statements are justified, and I shall have to deal with them more fully in the part of this paper devoted to that Order.

We are thus faced with the situation of having to choose between the limited outlook, but greater accuracy in detail, of the solution offered us by the specialist in one Order, of whom I take Meyrick as a conspicuous example, since he shows in a most remarkable degree the combination of both these characteristics; and the wider outlook, but occasional inaccuracy in detail, of the solution offered us by the non-specialist, whose aim should be to regard all the Orders coming under his review as equally entitled to careful examination and consideration.

It will be at once obvious, without any further argument, that neither of these alternatives is entirely satisfactory. Before we can deal satisfactorily with the phylogeny of a group of Orders, we must attain, as far as possible, to the specialist's knowledge in every one of them. Such knowledge, in the present advanced state of Entomology, is unattainable within the lifetime of any single man. We must, therefore, ask ourselves, firstly, whether we may legitimately attack a problem of such magnitude, equipped with anything less than the maximum of attainable knowledge on all Orders; and, secondly, whether, if this first question be answered affirmatively, we can indicate with any certainty which portions of that knowledge are essential, and which are not.

Now there will be, in any group of Orders, some which show definite specialisation above the others; as, for instance, the Lepidoptera and Diptera above the Trichoptera and Mecoptera. All entomologists are agreed upon this. Is it more necessary to attain to the specialised knowledge of the lower groups, or of the higher groups? It will be seen that Meyrick was a specialist in the higher of the two Orders which he discussed, while the same is true of Handlirsch, in a more general way, since he, everywhere, shows a far more intimate knowledge of the Lepidoptera and Diptera, but especially of the latter, than he does of the Trichoptera and Mecoptera. Would it not be preferable for the author, who is to attempt a satisfactory solution of this problem, to throw the main weight of his studies on to the side of the more archaic Orders, which, unfortunately for the progress of Entomology, have been so neglected for many years, and to be content to attain to a first-hand knowledge of only the more archaic types within the more highly specialised Orders?

I believe that this question must be answered in the affirmative, for some very good reasons. Firstly, the knowledge of the more archaic Orders is the only sure foundation upon which the Phylogeny of the higher Orders can be built. Any attempt without this knowledge is merely building up a house without laying secure foundations. Secondly, the connections sought for in the tracking out of the ancestry of the higher Orders must be those between some members (either existing or extinct) of the more archaic Orders and the *least specialised families* of the higher Orders. Thirdly, if at any time the problem transcends the attainable bounds of knowledge of the investigator who has adopted the course here advocated, he can always call in the advice of the specialist, who possesses just that very type of knowledge, in his own group, which would render the Phylogenist's task too overwhelming for him, on the principle of "not being able to see the wood for the trees." And, finally, there are already, in Entomology, specialists enough in all the higher

Orders; so that the chance of being brought to a full-stop, because nobody in the world can supply the gap required, is so unlikely a possibility that it may be dismissed without further thought.

That being so, I decided that the investigation into the Phylogeny of the Panorpoid Complex was a task that I might venture to undertake, and that its difficulty and immensity would be more than compensated for by the advantage to Entomology in general, if a satisfactory solution could be found. Having, then, decided to confine myself to researches within the limits indicated in the previous paragraph, I have carried out an exhaustive survey of the older Orders under review, viz., the Planipennia, Megaloptera, Mecoptera, and Trichoptera, and have been content to study, in the immense Orders Diptera and Lepidoptera, mainly the older families only. The survey has been extended far enough to give me some idea of the position and inter-relationships of all the important families of each of these Orders; but intensive study has been chiefly confined to the older families, together with other more specialised types in which I thought I could recognise characters of value as evidence on the question at issue. Further, it will be at once evident that the equipment of the author who attempts to solve this immense problem will not be complete unless he masters what there is to know about the Fossil Record of the Orders in question, and of their possible ancestral Orders. This also I have endeavoured to do. The fortunate circumstance of my having in my hands a large amount of new and unique material of this kind from the Permian and Triassic strata of Eastern Australia has been one of the chief factors in my decision to undertake this task; indeed, it has almost imposed the obligation upon me, since nobody who has not studied these fossils could possibly be so favourably placed for discussing this question as I happen to be, simply through this great good fortune.

It will, I think, be readily granted that the *Order* is the only satisfactory unit upon which a study of this kind can be based. We have, therefore, to consider what view of an Order we must take, in dealing with it as a separate unit in a paper such as this.

Now there are, in any given Order, many diverse groups. Some of these will exhibit very high specialisations in one or more directions; others will show unexpected archaisms, which may make it exceedingly awkward to frame a comprehensive definition of the Order. As an example of this, we may take the evolution of the mouth-parts within the Order Lepidoptera. In the great majority of the families within this Order, the mandibles are absent, the maxillary palps absent, the galeæ produced into a long sucking-tube or haustellum, and the labial palps present and more or less highly specialised. But, in the *Micropterygidæ*, the mandibles are present, as are also the typical maxillæ of older Holometabolous Orders, with five-jointed palpi, and unspecialised galeæ and laciniæ There is, therefore, no reason, from the Phylogenetic view-point, why we should not consider the Lepidoptera as, *at bottom*, essentially a mandibulate Order, when we come to discuss its relationship with the other Orders of the Panorpoid Complex.

It must, therefore, be evident that, for the purposes of this paper, the usual definitions of Orders to be found in text-books not only will *not* serve our purpose, but may actually be misleading. I propose to overcome this difficulty by the use of Archetypes (German, *Ur-typus*). For each Order that comes under review, we must define an archetype, which shall include in itself all the most archaic characters found within the Order. Having done this, we may reasonably discuss the relationships of the archetypes of the various Orders, with some prospect of a successful issue.

In following out this line of argument, we can lay down two guiding principles:—

(1) The Phylogeny must not be determined from one set of characters only (*e.g.*, wing-venation), however important that set of characters may be. But it must be determined by a review of as many characters as possible.

(2) The greatest care must be exercised in the determination of the characters of the Archetype. For instance, in the case of the jugum and frenulum in Lepidoptera, it is not sufficient to adopt the jugum as the more archaic character, merely because

it is found in those Lepidoptera which have the most archaic wing-venation. If a mistake is made here, the whole Phylogeny is bound to go wrong. As a corollary, it should follow that characters in which the evidence of archaism or specialisation may be uncertain, with a division of opinion upon the point amongst those entomologists who have studied it, must be either definitely cleared up by means of new evidence, or they must be entirely omitted from the argument.

The Determination of Archetypes.

We may exhibit this principle as follows :—

Let a, b, c, d, ... etc., represent a series of characters which are constant throughout the Order in question.

Let p, q, r, s, ... etc., represent a further series of characters which are not constant throughout the Order, but show definite lines of evolutionary advance in one or more directions.

Taking any one of these characters p, after examination of its structure in various families, let P represent the most archaic condition, while p', p'', etc., represent various specialised conditions of the same.

Any family within the Order can now be defined by the characters

$$a, b, c, d, \text{etc.}, \ldots\ldots p, q, r, s, \ldots\ldots \text{etc.},$$

where p can have any of the values P, p', p'', etc., q any of the values Q, q', q'', etc., and so on.

For instance, one family may be defined by

$$a, b, c, d, \ldots\ldots p', q'', R, s''', \ldots\ldots$$

The Archetype of the Order, which may or may not still be existing (the greater the number of characters taken, the less likely is it to be still existing) will be defined by

$$a, b, c, d, \ldots\ldots P, Q, R, S, \ldots\ldots$$

The Determination of the Phylogeny of separate Orders.

The same principle as above may be followed in this case, *provided we take the characters of the Archetype as the characters of the Order it represents*, for the purposes of the Phylogeny.

In this case, the characters a, b, c, d, ... etc., which were constants throughout any single Order, will now be variables for the different Archetypes; also P, Q, R, S, ... not having the same values for different Orders, we may omit these letters, and consider that the whole series of characters is comprised in a single (longer) series of variables a, b, c, d, e, f, ... etc. Taking a group of Orders, we may now represent the most archaic value of the character a by A, while a', a'', etc., represent various specialised conditions of the same. Then we shall be able to write the Archetypes of different Orders in this way

Archetype of Order 1:—A, b'', C, d', e', F, g'' . . . (say).
Archetype of Order 2:—a', b', C, d'', E, f''', G . . . (say).
Archetype of Order 3:—A, B, c', D, e'', f', g' . . . (say); and so on.

The condition that any one Order may be *ancestral* to another can now be determined by comparing the Archetype of the supposedly higher Order with any supposedly ancestral group lying within the bounds of the Lower Order. But, as the characters of the Archetype of the supposedly ancestral Order are even more archaic than those of the supposedly ancestral group lying within that Order, the determination may be made, once for all, by comparing the Archetypes of the two Orders. The following rule may be laid down:—

The condition that one Order may be truly considered ancestral to another, is that *there must not exist a single character in the Archetype of the former, which is more highly specialised than the corresponding character in that of the latter.*

For example, consider the case of Orders 1 and 3 above. The character A is common to both Archetypes. For the character b, the Archetype of Order 3 is the older (B against b''). But for the character c, the Archetype of Order 1 is the older (C against c'). Hence, clearly, neither of these two Orders can be considered as ancestral to the other; and we must go back, for their common ancestor, to an Order (probably no longer existing) whose Archetype shows the characters A, B, C, ...

The Recognition of Embryonic Structures.

It would seem necessary here to call attention to the fact, which seems to have been quite ignored by most of those entomologists who have not studied other Classes of Animals, that it is not necessary to be able to trace back a structure to the embryo without a break, in order to prove that it is derived from an embryonic structure. Particularly does this apply to appendages within the Phylum Arthropoda. Examples of this are the well-known observations on the re-development of limbs from latent embryonic rudiments in Crustacea, *e.g.*, the mandibular palp in Decapod larvæ, and the maxillipedes of the Stomatopoda. In fact, the rudiments may appear in the embryo, disappear later on, and then reappear again in the imago, as in the case of the thoracic legs of the genus *Chalicodoma* and other genera in the Order Hymenoptera.

Thus we see that it is *not* sufficient proof that a structure is not derived from an embryonic rudiment to show that it does not develop directly from that rudiment; whereas, it *is*, most certainly, quite sufficient proof that it is so derived, if we can trace it up from the embryo, through the larva and pupa, without a break, to the imago (or, if the structure in question is only a larval one, then it need only be traced from the embryo to the larva).

We may take, as an example of this, Lubbock's observation upon the development of the lateral gills in *Chloëon*, which, he proved, did not begin to develop until the third instar of the larva. Many entomologists have used this as proof that these gills cannot be homologous with the original segmental abdominal appendages, which are represented in the embryo, and then disappear. This argument is quite fallacious, and must be carefully avoided, since it is a frequent temptation to use it. Further, there is another potential fallacy in this kind of argument. *Chloëon* is a highly specialised member of the Order Plectoptera. May it not be quite possible that the break between the embryonic appendages and the formation of the gills, which is so conspicuous in this genus, may be very much reduced, if not completely removed, in the case of the development of the larva of some much more archaic type, such as *Oniscigaster*, not yet studied ?

Meyrick's Law.

In 1893, Comstock (**1**) gave the name "Meyrick's Law" to the following statement, which was first enunciated by Meyrick in 1884:—"When an organ has wholly disappeared in a genus, other genera which originate as offshoots from this genus cannot regain the organ, although they might develop a substitute for it."

Stated in this manner, this law may be accepted, provided it is clearly understood what its limitations are. These may be stated as follows:—

(1) It must be capable of proof that the organ in question has *wholly* disappeared from the assumed ancestral genus. For instance, a concealed rudiment of an organ may reappear, after a more or less lengthy period of suppression during the course of evolution of the group. It will be clear that this fact alone must make the application of the law exceedingly problematical, except in the case of very simple and easily examined structures or organs.

(2) Great care must be exercised in determining what is to be regarded as a *substitute* for an organ, as contrasted with an actual redevelopment of the original organ from a concealed rudiment.

(3) The converse of the law is not necessarily true; *i.e.*, if a genus B shows the loss of certain organs in comparison with another genus A, we are not entitled to state, without further evidence, that B is descended from A; we may only state that A is more archaic than B in respect of the characters in question.

How little the importance of the safeguards in the original statement of this law has been regarded may be gathered from Meyrick's own later work. In 1895 (**3**), we find him enunciating three "laws" as his guiding principles in the determination of the Phylogeny of the Lepidoptera. These are stated as follows:—

"(1) *No new organ can be produced except as a modification of some previously existing structure.*"

"(2) *A lost organ cannot be regained.*"

"(3) *A rudimentary organ is rarely redeveloped.*" (p.10).

Of these, No.2 is Meyrick's Law restated without its original safeguards. This, taken in conjunction with the other two, forms a very generalised statement covering a very much wider field than the original one, and open to far graver objections. As regards Law No.1, this can only be accepted as true in its very widest sense, *i.e.*, that there must be pre-existing living material, or cells, as a basis from which any new structure is to be developed; and, in that sense, it ceases to have any value, and becomes a truism. With respect to Law No.2, this ceases to be true when the restrictions contained in the original statement of the law are removed. To mention only one obvious example. The thoracic legs of certain Hymenoptera (e.g., *Chalicodoma*) appear in the embryo; they then disappear throughout larval life, but reappear again in their complete form in the imago. Thus, in this case, as in many others, "a lost organ *is* regained"; and a bald statement to the contrary is not only not a law, but it is not true. Moreover, it may not be argued that the law is true when applied to Phylogenetic problems only, and not to Ontogeny. For, if there is any truth in the Biogenetic Law at all, it is certain that what occurs in Ontogeny is of the same nature, and governed by many of the same laws, as what occurs in Phylogeny; and if we frequently find that lost organs *are* regained in the course of Ontogeny, then it follows that we may by no means assert that the same possibility cannot hold for Phylogeny. With respect to Law No.3, it is only necessary to remark that there is probably no Phylum in which rudimentary organs are so often redeveloped as in the Arthropoda, and that this is particularly true of appendages.

It would seem much wiser to do without any attempt to formulate laws (so-called) for the solving of Phylogenetic problems, and to treat each case, as it presents itself, upon its own merits. In most cases, for instance, it is quite capable of definite proof that, in a given phyletic series, an organ originally present has been lost, and never regained in any of the descendant genera. In other cases, not so numerous it is true, it is capable of proof, by reference to palæontological evidence, that lost organs have been regained, or, perhaps, that organs which, on the strict application of Law No.2, would have to be regarded as originally present and subsequently lost, are really new developments not present in the ancestral form. In such cases, a rigid application of the law would result in a complete inversion of the phylogenetic conclusion.

Meyrick himself applied his law chiefly to the problem of wing-venation in the Lepidoptera. In a case like this, where almost the whole course of evolution is towards reduction and simplification, there is not much danger in its use. Yet even here caution is necessary. It is not true, for instance, that veins which have once been lost cannot be re-developed; nor is it true that new cross-veins cannot be formed in a wing-area in which no such structures existed in the ancestral form. One has only to examine the tracheation of the pupal wing in the Lepidoptera to see that there is an immense field of possibilities in both these directions, owing to the persistence of the finer tracheæ, ramifying in all directions beneath the wing-membrane. As long as these tracheæ persist, so long must the possibility of an imaginal venational meshwork reappearing be held to exist. Moreover, in a case in which the wing is changing its shape, so that a certain part of it may become broadened, it is exceedingly likely that one or more of the tracheæ underlying the veinlets of this area will become lengthened and strengthened, so that it may eventually lead to the replacement of an original short veinlet by a longer oblique branch, which, on Meyrick's interpretation, would have to be regarded as an original archaic branch of the main vein from which it springs. One of the best examples of this is the effect of the widening of the costal area in the *Psychopsidæ*, in which an originally fairly simple series of veinlets has become greatly lengthened and enlarged, most of its units branching many times; and all of them connected together by newly developed series of cross-veins, which were certainly not present in the ancestral form.

The above example shows us that, even in so restricted a study as that of Wing-Venation, Meyrick's Law can only be used with great caution. It must be restricted to *areas of the wing that are undergoing reduction.* In the present state of evolution of the Insect-Wing, it is certainly true that the tendency is towards reduction in the great majority of cases. But this cannot always have been the case. Bearing in mind the complex nature of the wing-venation in the most archaic types of insects, we are bound to conclude that, at the beginning of the evolution of the wing, there must have been a period of great enlargement, with a rapid and abundant production of veins in all parts (following upon the rapid increase in the tracheation of the developing organ). After this had reached its maximum, there began a period of arrangement and reduction, during which the very beautiful and perfect wing-types at present existing were evolved. We may term the process by which any part of a wing becomes broadened, with consequent production of further venation in that area, Platygenesis (Gr. πλατύς, broad); while the opposite process, in which the wing-area in question becomes reduced or narrowed, with consequent reduction or elimination of some of its existing venation, may be termed Stenogenesis (Gr. στενός, narrow). The development of the costal space in the *Psychopsidæ*, of the enlarged anal area of the hindwing in Anisopterid Odonata, and of the wide *anal fan* in the Orthoptera, Perlaria, and other insects, are good examples of Platygenesis; while the process of Stenogenesis can be followed out very fully in such an evolutionary series as the Diptera Nemocera.

Scheme of the Work.

We have already stated that phylogenetic conclusions, to be acceptable, must be based upon an examination of as many characters as possible. In undertaking an analysis of a large number of characters, two methods of procedure are possible. We may either select each Order in turn and study its characteristics fully, with a view to the determination of its Archetype; or we may select any given set of characters, as, for instance, those offered by the Wing-venation, and study them as they are exhibited throughout the whole of the Orders under discussion; proceeding to deal with other sets of characters in subsequent parts of the work.

This second method must obviously be the one chosen, for only by it can the necessary comparisons be made between the same sets of characters in different Orders. Thus we have to postpone the definition of Archetypes until the whole of the characters selected have been surveyed; and the final decision as to the phylogenetic relationships of the various Orders will not become fully apparent until the work is completed. Meanwhile, it seems advisable to select the characters for study in such a way that the work can be subdivided up into a series of parts, each complete in itself, and suitable for separate publication. Working on these lines, we may conveniently begin with those characters which have been most used in phylogenetic discussions, and proceed to deal with the rest in a definite order. Thus we shall at first confine our attention to a study of the Wings alone, and these will occupy two or more parts of the work. Next to these, we shall take the Mouth-parts. Subsequent parts will deal with other imaginal structures; and, lastly, the structure of the larva and pupa will be reviewed. As regards the structure of the egg, and the Embryology, it is to be regretted that so little is known about the latter in the case of the more archaic Orders. As our knowledge stands at present, the evidence available on this point, for the purposes of this paper, is so incomplete, that it can have little bearing upon the main result.

The investigations into this problem were actually begun about two years ago, and are still going on. I feel that I can safely leave the completion of the more specialised parts of the work to a later date; because, if I waited until they were all finished, the main conclusions of this work would not, perhaps, see the light of publicity for some years. The results already attained are, to my mind, of such importance that I have no hesitation in placing them in the hands of the scientific public, and their value will not be lessened by delay in the completion of the whole fabric of my work.

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Note.—A bibliography will be supplied for each part, with the reference numbers running consecutively; but those papers which are not referred to in any given part will be omitted from the bibliography for that part.